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Cover Page Footnote

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Evolution of Cooperation in Mobile Populations

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Abstract

We consider a finite, fixed-size population of mobile cooperators and free-riders. A cooperator is an individual who, at a cost to itself, provides benefits to any and all individuals in its vicinity, whereas a free-rider does not provide any benefits and thus pays no cost. Individuals are free to move to maximize their payoff, and our model allows for the interactions among multiple individuals at the same time. Using Gillespie's algorithm, we build an exact stochastic simulation of this continuous-time Markov process and find that decreasing the individuals' mobility or decreasing the size of the interaction neighborhood promotes the fixation of cooperators in the population.

Keywords: Evolution of cooperation, mobility, stochastic simulations

1 Introduction

Understanding the emergence and persistence of cooperation among selfish individuals has sparked extensive studies in evolutionary game theory [39, 5, 37, 27, 41]. As conventionally understood, cooperators are individuals who pay a cost in order for another individual to receive a benefit, while a free-rider (or a defector) is an individual who does not provide any benefits, and thus pays no cost, but can receive benefits if offered. In infinite and well-mixed populations, free-riders are favored over cooperators as all individuals receive the same benefits but cooperators alone incur the cost. Yet, cooperation can be found everywhere around us, and it builds and sustains many biological, social, and economical systems [6, 28].

The prisoner's dilemma game [5] is a classical model for the evolution of cooperation for pairwise interactions; however, real interactions typically involve multiple individuals. In response, multi-player games were introduced into biology models [31, 8, 11], and recent studies have gone into greater details [15, 16]. Furthermore, games of public goods, which are multi-player analogues of the Prisoner's dilemma, have also been studied in [17, 26, 35, 20, 40, 36, 45, 21].

Nowak in [28] discusses several mechanisms for the evolution of cooperation such as network reciprocity. In [29] it was demonstrated that, within a fixed spatial structure where individuals can interact only with their closest neighbors, cooperators can help each other out and survive by forming clusters. The effect of spatial structure has been studied in [33, 34]. The cluster formation

helps protect the cooperators against potential invasions made by the free-riders even in mobile populations [13]. Once individuals can move, the corresponding interaction structures can change, analytical models such as [30] no longer apply, and new models must be developed. For example, Axelrod in [5] considered individuals on a two-dimensional square lattice, where interactions would only happen within local neighborhoods. Vainstein et al. [44] extended the model of Nowak and May [29] by considering a regular lattice where some vacant sites permit the individuals to diffuse easily; see also [32, 38, 7, 4, 48, 22, 43, 1] for other models of dynamic networks.

The evolution of cooperation in mobile populations has recently been studied in [12, 46, 3]. In our paper, we consider a finite, fixed size population of mobile individuals that can potentially provide benefits to all individuals in their vicinity. Individuals are either cooperators or free-riders, the determination of which is made at the start of each simulation. We allow the individuals to move in a directed fashion towards places with higher payoffs, i.e. generally towards cooperators. Using Gillespie's algorithm [14], we build an exact stochastic simulation and study how mobility—defined as the average number of individual movement events for every reproduction event—and the neighborhood size of an individual affects the evolution of cooperation.

2 Methods

We consider a continuous time Markov chain process on a population of N individuals I_1, \dots, I_N occupying positions P_1, \dots, P_N on a 1-dimensional lattice of length L with pe-

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riodic boundaries. At the beginning, the positions of all individuals are chosen at random and, as in [13], each individual is randomly assigned with equal probability to be either a cooperator (C) or a free-rider (F). We allow multiple individuals to occupy the same position in space.

Let b be the benefit and c be the cost for cooperation. We say that the individual I_m is in a vicinity (or neighborhood) of I_n if their mutual distance is no more than the neighborhood radius, r . The neighborhood of individual I_n is thus the interval consisting of $2r + 1$ points $(P_n + d \bmod L)$ for $d = -r, \dots, -1, 0, 1, \dots, r$.

Given the positions and types of the individuals, we define the payoff of an individual I_n by

$$p_n = b \cdot C_n + \frac{1}{C_n + F_n} - c_n \quad (1)$$

where

$$c_n = \begin{cases} c & \text{if } I_n \text{ is a cooperator,} \\ 0 & \text{if } I_n \text{ is a free-rider} \end{cases} \quad (2)$$

stands for the actual cost of giving or not giving the benefits; C_n and F_n are the numbers of cooperators and free-riders, respectively, in the vicinity of individual I_n , including the individual I_n itself; and the term $\frac{1}{C_n + F_n}$ represents the competition for local resources among all the individuals. When no cooperator is present in the system, this causes the individuals to distribute practically uniformly over the environment.

Different positions of an individual yield potentially different payoffs. When individuals are allowed to move within the environment, it is thus plausible that they will tend to move towards places with higher payoff.

Our Markov chain process consists of two types of events. One event is a movement of an individual, another one is a reproduction of an individual. The mobility of an individual is characterized by the average number of individual movement events for every reproduction event. We assume that an individual “samples” all possible places it can move to from its current position and then picks a new place with a probability positively correlated to the difference between the payoff at the potentially new place and its current position. Specifically, the propensity of an individual I_n to move from P_n to $P_{n'}$ is $\exp(p_{n'} - p_n)$, where p_n is given by (1) and $p_{n'}$ would be given by a same formula assuming the position of I_n would be $P_{n'}$ and not P_n . In order to minimize the number of different parameters of our model, we assume that individuals can simply move one place left, stay in a same place, or move one place right, but in theory, larger and more general moves are possible. When a_1, \dots, a_m represent all propensities of all potential moves of all individuals, a move corresponding to a_k happens with probability $a_k / (\sum_{l=1}^m a_l)$. In general, the individual that can increase its payoff most is the one that most likely moves;

however, an individual can move to a position with lower payoff. Such a move is very unlikely, yet such a “non-optimality” of the movement is needed to guarantee for the individuals to be able to find the global optima and not get trapped in the local ones.

For reproduction, we consider “birth-death” updating (see for example [23]). First, with a probability proportional to the individual’s payoff, we randomly choose an individual to be reproduced. If the payoff of an individual I_n is p_n given by (1), then an individual I_m is chosen for reproduction with probability

$$\frac{\tilde{p}_m}{\sum_{n=1}^N \tilde{p}_n} \quad (3)$$

where the adjusted payoff, \tilde{p}_n of an individual I_n , is defined by

$$\tilde{p}_n = \tan^{-1}(p_n) + \frac{\pi}{2}. \quad (4)$$

This adjusted payoff, \tilde{p}_n , is used in place of p_n in (3) to make sure that (a) individuals with $p_n < 0$ can reproduce and (b) individuals not in the cluster of potentially many cooperators can reproduce. Without such an adjustment, cooperators would drive free-riders to extinction very soon after several cooperators aggregated.

The offspring inherits from its parent the strategy (cooperator or free-rider) and it is placed randomly close to the parent (either just next to the parent or at the same place as the parent). Finally, a random individual of the original population (potentially including the parent) is culled to maintain the population at constant size.

We simulate the above described Markov chain process by the Gillespie’s algorithm implemented in Matlab [25] (see [10] for a general implementation of the algorithm in Matlab). We run the simulation until all individuals are either cooperators or free-riders and we repeat such runs 10^4 times. The fraction of times cooperators win is called the fixation probability of cooperators.

Our simulation worked as intended. See for example Figure 1 showing the population of 4 individuals, 2 cooperators, and 2 free-riders. The individuals move randomly, but with a general tendency to aggregate around cooperators. The free-rider starting originally around position 37 finds the cooperator from position 45 relatively fast around time 10. The cooperator tries to escape and due to an (intended) non-optimality of the movement, the escape is successful as the free-rider did not follow at first, only to join the same cooperator some later around time 60. Around the time 65, two cooperators join and form a group. This increases their payoff and (by a chance) one of them is selected for a reproduction. By a chance, a free-rider originally from position 80 is killed and the new cooperating individual is placed within the cluster of cooperators. The cluster of 3 cooperators

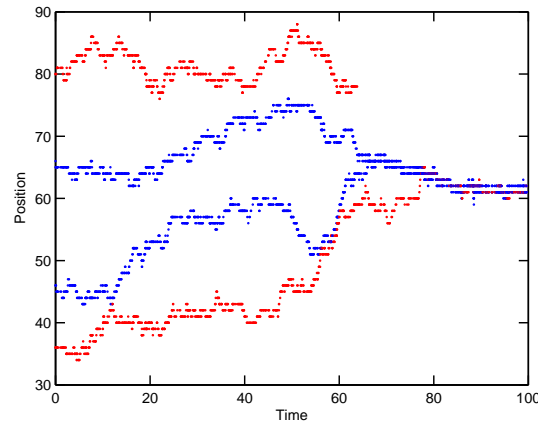


Figure 1: Evolution of the population and positions of the individuals in time. Cooperators are blue, $N = 4$, $L = 100$, $b = 2$, $c = 3$, $r = 1$, and mobility = 100.

is strong enough so that they rarely break up and thus keep together. The remaining free-rider finds the cluster around the time 80 and stay with it as well. There is another reproduction event at time 100 at which point a cooperator replaces the free-rider and the simulation ends.

3 Results

We have run the simulation for $N = 30$, $L = 100$, $b = 2$, $c = 3$, neighborhood radius ranging from 1 to 49, and mobility ranging from 0 to 10. We replicated each data point 10^4 times to rule out a stochastic noise as much as possible. The results are demonstrated in Figure 2 and can be summarized as follows:

1. For a reasonably small neighborhood (in our case smaller than $2/5$ of the total environment), decreasing the mobility increases the fixation probability of the cooperators.
2. Increasing the size of the neighborhood (in our case to about $1/2$ of the total environment) decreases the fixation probability of the cooperators.
3. For larger neighborhood sizes (in our case $2/5$ or more of the total environment), neither the mobility nor the neighborhood size has any significant effect on the fixation probability of cooperators.

The effect of the neighborhood size is easy to understand within the framework of existing literature. The fixation probability of cooperators is strongly linked to the presence of clustering [13, 33]. Within our framework, individuals are allowed to move and clusters are formed relatively fast. As the neighborhood size increases, the

formed clusters contain more individuals, and thus, as shown in [45] (see also [9, 18]), the cooperation is harder to achieve.

Also, everything indicates (although we did not collect appropriate exact data) that as mobility increases, larger and larger clusters can form even in relatively small neighborhoods (since in our model multiple individuals can occupy the same spot) which would explain the negative effect of mobility by results in [45] as above.

4 Discussion

We have created an exact stochastic simulation for a mobile population consisting of cooperators that are able to enhance the quality of the environment, but have to pay a cost for doing so, and free-riders that do not modify the environment themselves but can benefit if others improve it. We observed that as either the mobility or the neighborhood size increases, the fixation probability of cooperators decreases. The simulations were computationally quite expensive (especially for large mobilities). However, we did run a smaller number of simulations while varying different parameters (such as dimensionality or size of the lattice, size of the population, benefits and cost of the cooperative behavior) and did not see any indication that our results above are violated.

The negative effect of the neighborhood size on the evolution of cooperation is relatively well understood, yet it is still complex. As the neighborhood size decreases, the probability of cooperators fixating increases, but the cooperators are potentially cooperating less (when the neighborhood size is 0, an individual cooperates only with those occupying the exact same place). It is therefore not entirely true that decreasing the neighborhood size

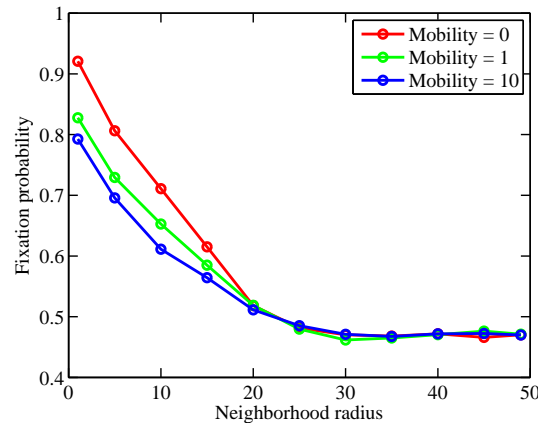


Figure 2: The dependence of the fixation probability of cooperators on the neighborhood size. Each data point is an average of 10^4 simulations. Parameters are $N = 30$, $L = 100$, $b = 2$, and $c = 3$. Radius of 50 represents the whole environment.

promotes cooperation. The effect of mobility on the fixation of cooperation depends heavily on the details of the model. Vainstein et al. [44] and Lin et al. [24] consider regular lattice environment where some sites are empty which permits the individuals to diffuse. In such a setting, Vainstein et al. [44] similarly found that increasing mobility promotes cooperation because it increases the likelihood of the formation of cooperator clusters and eventually dominate the population. At the same time, mobility reduces the competition for local resources and helps to promote cooperation [2]. Moreover, Jia and Ma [19] demonstrate that a higher movement speed enhances cooperation within a very large environment, but within very small regions, increasing the movement speed actually reduces the cooperation level. In our setting, mobility is inversely proportionate to the reproduction rate that has been used in work of others. For example, [42, 47] show that a wide range of reproduction rates can enhance cooperation, while really fast and slow reproduction rates can hurt cooperation no matter what is the interaction neighborhood size.

We recognize several future directions in which research could follow and help further our understanding of cooperation. In this paper, we focused on two primary parameters, neighborhood size and mobility, but there are other model parameters whose variation and interplay also need to be considered. The cost of cooperation, benefits provided, and heterogeneity of the environment could all be contrasted in different studies. Also, we conjecture that the key deciding factor for the evolution of cooperation in our setting is the average number of individuals in the formed clusters. Namely, if a change in the parameters causes the mean cluster size to increase, the fixation probability will decrease.

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